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THE ANATOMY AND HISTOLOGY OF THE MALE REPRODUCTIVE SYSTEM OF CAMPONOTUS PENNSYLVANICUS DEGEER (FORMICIDAE, HYMENOPTERA)

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NINETEEN FIGURES

Studies on the anatomy of the male reproductive system in ants are few, and our information needs to be augmented considerably before the functioning of this system can be fully understood. One of the first workers to investigate the internal anatomy of ants was Meinert (1861), and his paper includes descriptions and figures of the anatomy of the male reproductive systems of *Formica rufa* and of *Myrmica ruginodis*. Forel, in his "Fourmis de la Suisse" (1874), devotes a small section to anatomical anomalies in which he reports observations on dissections of a gynandromorph of *Formica truncicola* and of an ergatandromorph of *Polyergus rufescens*. His account merely lists the organs and their arrangement; no detailed information is included because of poor preservation of the specimens. Adlerz (1886) has given a more complete anatomical description of the male system of *Camponotus ligniperdus* and has figured the male systems of *Leptothorax acervorum*, *Anergates atratulus*, and *Formicoxenus nitidulus*. Janet ('02) made a rather detailed study of the anatomy of the male system of *Myrmica rubra*. However, the histology of the organs is neither described nor figured in his illustrations of the system. Muckerjee ('27) has described the anatomy of the male reproductive system of *Dorylus labiatus* in his paper on the vespoid affinity of the Dorylinae. Clausen ('38), in

his comprehensive study of the genitalia of the ants, describes the relation of the ejaculatory duct to the inner valves of the genitalia in *Formica rufa*. He was the first to discover, in the ejaculatory duct of this species, the chitinous wedge, which he refers to as the constricting wedge or sperrkeil. More recently Marcus ('53) has briefly described the male system in *Dorymyrmex emmaericaellus* and the seminal vesicles and ejaculatory duct in *Acromyrmex sylvestrii*. He mentions that there is a chitinous angle in the posterior end of the ejaculatory duct of this latter species, which opens anteriorly and has its apex directed posteriorly.

This review of the literature makes it apparent that the anatomy of the male reproductive system is known for only a very few of the numerous genera and species of ants and that no comprehensive or detailed histological study has ever been reported for the organs of this system. This paper describes the anatomy and the histology of the male reproductive system of the carpenter ant, *Camponotus pennsylvanicus* DeGeer, and also reports observations from males collected during a nuptial flight.

MATERIAL AND METHODS

The male ants used in this investigation were collected from nests at Yonkers, New York. The methods of preparation of the material have been reported in an earlier study of the workers of this species (Forbes, '38). The sections were stained by means of the Feulgen technique counterstained with light green, with standard alum-haematoxylin and triosin, and with Verhoeff's elastic tissue stain and triosin. The entire system and organs of the system were dissected out and stained by Lynch's precipitated borax-carmine method (Galigher, '34). The Verhoeff's stain was used to determine whether the capsule covering the testes contains fibers which would be selectively stained; the results were negative. The males on nuptial flight were collected together with queens as they were swarming in the late afternoon of July 9, 1936. These specimens were fixed in alcoholic Bouin's

fluid, the abdomens were processed by the n-butyl-dehydration method reported in Lee ('37, sect. 127), and sections were cut at 10 μ. The sections were stained with standard alum-haematoxylin and counterstained with triosin. The material prepared by this method sectioned very well. A Promar drawing apparatus (Siebert, Wetzlar) was used as an aid in the preparation of the drawings for the paper. The author extends his thanks to Mr. Alfred Teoli, a former student in the department, for his help with figures 1 and 5 of this paper.

OBSERVATIONS

The male system consists of the testes and vasa efferentia, the vasa deferentia, the seminal vesicles, the ejaculatory duct, the aedeagal bladder, and the external genitalia (figs. 1 and 2).

The testes lie dorsal to the ventriculus of the digestive system in the 4th or the beginning of the 5th abdominal segment, one on either side of the midline. Each testis is composed of 12 to 16 small, spherical saccules, the testicular follicles. Each follicle opens into a short duct, the vas efferens. The vasa efferentia in turn lead into a common duct, which continues into the wider vas deferens. The first portion of each vas deferens is looped and twisted, but it continues in a rather straight, posterior, ventral direction to open into the posterior, ventral, mediad surface of the seminal vesicle. The posterior end of the vas deferens is slightly constricted just before it enters the seminal vesicle. The testes and the anterior, convoluted portions of the vasa deferentia are covered by a single, fiber-like capsule, which is composed almost entirely of intertwined tracheal branches. This single capsule is usually constricted in the midline between the testes (figs. 1 and 2).

The seminal vesicles are large, swollen tubes which extend from the first third of the 5th abdominal segment to the beginning of the 7th segment. Posterior to the entrance of the vasa deferentia, the median surfaces of the seminal vesicles

come together and touch, and the diameter of each vesicle is reduced. The posterior portions of the seminal vesicles unite to form a single duct, the ejaculatory duct, which opens on the dorsal, posterior surface of the aedeagal bladder (figs. 2 and 4).

The diameter of the ejaculatory duct is not uniform throughout its length. Laterally, the duct enlarges slightly for about two-thirds of its length, and then it tapers posteriorly (fig. 18). The height of the duct enlarges one-third to one-half for the same two-thirds of its length and then reduces (fig. 4). In the lumen of this bulge of the ejaculatory duct, there is found a chitinous, Y-shaped wedge, the sperrkeil of Clausen ('38) (fig. 3). The arms of the Y arise from ventrolateral, epithelial folds of the duct. The base of the Y extends posteriorly for a short distance and ends at the opening of the ejaculatory duct into the aedeagal bladder. This base is not attached to any part of the duct wall; it extends free in the lumen. Measurements have been made of the width and the length of this wedge. The width has been taken as the distance between the anterior ends of the arms and the length as the antero-posterior distance taken at right angles to the first measurement and passing through the point of the wedge. The measurements of 9 wedges show the average width to be 180 μ with variations from 151.2 μ to 216.0 μ and the average length to be 300 μ with variations from 270 μ to 324 μ.

The aedeagal bladder is a large sac, which lies in the 7th and 8th abdominal segments, ventral to the posterior ends of the seminal vesicles and the ejaculatory duct (fig. 1). The posterior opening of the aedeagal bladder is dorsally situated, and it continues into the sperm gutters on the inner, genitalic valves (fig. 4). The arrangement and the anatomy of the valves of the external genitalia have already been described (Forbes, '52).

Testes and vasa efferentia (figs. 2 and 5). The cells which compose the testicular follicles are polyhedral or pyramidal in shape, they are arranged as a single layer around an indistinct central lumen, and they are enclosed peripherally by

a distinct basement membrane. Thin, twisted, cytoplasmic extensions from the free surfaces of these lining cells project into the lumina of the follicles and render them indistinct. The nuclei of these cells vary in size, in the density of the chromatin material, and in the amount of chromatin material present. The membranes of many nuclei are very thin and appear to be breaking down. This indicates that nuclear changes are occurring. Some follicular cells, usually the ones at the blind end of the follicle, appear to be composed of a mass of fine, indiscrete granules. This granular mass is slightly less acid in its staining reaction than the cytoplasm of the follicular cells. In addition, a very fine granular mass is situated over the free end and somewhat surrounding each testis follicle. This granular mass is loosely attached by granular strands to the basement membrane of the free end of the follicle around which it lies. These granular strands often go through the follicular basement membrane and join with the granular mass within the follicle. One or a few small, compact nuclei and occasionally a large, granular nucleus are embedded around the edge of each granular mass. Sections of the heads of spermatozoa can be seen scattered in the lumina of the follicles, intertwined with the cytoplasmic extensions, and embedded in the free surfaces of the cells. Small muscle fibers are loosely entwined around only the attached ends of the testis follicles, never around the blind ends of the follicles. Some of these muscle fibers might be branching fibers.

Each testis follicle continues into a short duct, the vas efferens. The vasa efferentia are composed of small, cuboidal-shaped cells with centrally located nuclei. These cells are built upon a distinct basement membrane. Cytoplasmic extensions from the free surfaces of these cells, similar to the extensions of the follicular cells of the testis, project into the lumina of the vasa efferentia. The vasa efferentia are collected into a short, narrow, common duct; this duct is reflected to form the much wider vas deferens. The small muscle fibers which are situated around the base of the testis follicles are continued around the vasa efferentia and the first part

of the vas deferens. The muscle fibers do not continue around the epithelium as it is reflected at the anterior ends of the vasa deferentia; this indicates no valve-like function at this region. Scattered spermatozoan heads are seen in the lumina of the vasa efferentia.

Capsule of testes (figs. 1 and 5). The capsule which surrounds the testicular follicles and their attached, granular masses is composed of a network of tracheae and tracheoles. The branching tracheae take convoluted and contorted directions between the felt-work of anastomosing bundles of tracheoles. Fusiform nuclei lie on and between the tracheoles in the bundles; the long axes of these nuclei are arranged parallel with the long axis of the bundles. Stellate-shaped cells with long, slender processes and fusiform or oval nuclei are found between the tracheae and the tracheoles and between branches of the tracheole bundles. These cells appear to constitute the connective tissue of the capsule. Occasionally there can be seen fairly large, multinucleate cells between the bundles of tracheoles. These cells are spherical or irregular in shape, the cytoplasm is slightly basophilic, and the number of distinct, granular nuclei within one cell can vary from 3 or 4 to 10 or 12. Fat cells surround the testicular capsule and help to hold the capsule with the testes in position. Occasionally a few fat cells are enmeshed in the bundles of tracheoles on the peripheral portions of the capsule, but fat cells are not a component part of the capsule. Dorsal peripheral bundles of tracheoles are fused with the ventral side of the dorsal diaphragm and apparently serve as suspensory fibers. No structures of the capsule were selectively stained with Verhoeff's elastic tissue stain.

Vas deferens (figs. 2 and 5). The epithelial layer of the wall of the vas deferens is composed of low, cuboidal-like cells built upon a distinct basement membrane. The cytoplasm is compact and non-vacuolate, and the flattened, oval nuclei lie in the lower portions of the cells with their long axes parallel with the bases of the cells. Scattered, obliquely arranged muscle fibers surround the epithelium. The number

of these muscle fibers increases toward the posterior end of the vas deferens. The vasa deferentia are filled with spermatozoa which are arranged spirally around the lumen of the tubes. This arrangement of the sperm gives the vasa deferentia a spirally-banded appearance in the unstained as well as in the stained whole mounts of these organs. The heads of the sperm point posteriorly, and the tips of the heads of many spermatozoa are embedded in the cytoplasm of the epithelial cells.

The testicular capsule completely envelops the convolutions of the anterior ends of the vasa deferentia and continues down the tubes in a much reduced condition. The capsule usually disappears in the posterior third of the vasa deferentia. However, in a few males dissected, this sheath-like, posterior end of the testicular capsule reached almost to the constricted, posterior regions of the vasa deferentia.

Constricted region of the vas deferens (fig. 6). The low, cuboidal-shaped cells of the vas deferens become columnar in shape as they continue into the constricted region. At the junction with the seminal vesicles, these columnar-shaped cells become taller and wider. The epithelium is built on a distinct basement membrane. The slender, compact nuclei usually are arranged in the central or basal portions of the cells, and the cytoplasm is highly vacuolate. The lumen of this region is completely filled with an acidophilic, non-cellular substance, which projects slightly into the seminal vesicle. his substance is secreted by the epithelial cells and acts as a plug to prevent the sperm from moving through the constricted region of the vas deferens into the seminal vesicle. About 4 layers of obliquely arranged muscle fibers surround the epithelium of this region. Although the muscle fibers are oblique in their arrangement, they are roughly grouped into an internal, circular layer and an external, longitudinal layer. At the junction of the vasa deferentia with the seminal vesicles, the muscle fibers are arranged circularly and obliquely as if to suggest a sphincteral function.

No differences have been observed in the anatomy and the histology of the testes, the vasa efferentia, the capsule of the testes, the vas deferens, or the constricted region of the vas deferens between the males collected in the nest during the spring and those collected on the nuptial flight.

Seminal vesicles (figs. 2 and 6). The high, columnar-shaped cells of the epithelium are built on a distinct basement membrane. The granular, ellipsoidal-shaped nuclei are located in the basal portions of the cells; their long axes are usually parallel with the basal membrane. The cytoplasm is practically completely filled with basophilic, secretion granules, which vary considerably in size. The free surface of some of the epithelium is flat and has the appearance of "typical" columnar cells. The free surface of the intervening areas, however, is quite irregular. In these areas, the cells are extended into long, branching, basophilic filaments which intertwine and form a fibrillar mass in the lumen of the seminal vesicle. The basophilic granules from the cells are mixed with the fibrils. This basophilic, granular and fibrillar secretion fills the lumen of the seminal vesicle. If a seminal vesicle is accidentally cut or punctured during dissection, the secretion flows out into the dissecting fluid as a milky white cloud. The epithelium is thrown into folds, some of which extend more than half way into the lumen. A well-developed muscle coat of 2 to 4 fibers in thickness encircles the epithelium. The muscle fibers are irregularly arranged obliquely and circularly; they are not disposed into layers. A few muscle fibers usually extend into the epithelial folds.

Toward the tapering, posterior ends of the seminal vesicles, the epithelial cells become lower in height. The cytoplasm still contains secretion granules, the free surfaces of the cells are still irregular and extend as short filaments into the lumen, and epithelial folds are still present. The muscle layer now becomes predominantly circular in direction. An occasional peripheral muscle fiber continues around the end portions of both seminal vesicles.

As the end portions of the seminal vesicles proceed toward the point at which they fuse to form the ejaculatory duct, the secretion granules in the cells disappear, and the free surfaces of the cells become flat; the filaments disappear. The cytoplasm in the cells becomes more dense, and many of the cells show small secretion vacuoles in the supranuclear cytoplasm. The epithelial folds flatten so that the lumina of the two tubes are quite regular in their outlines. A few circular muscle fibers surround and separate the epithelium of the two ducts, and a few, circular, peripheral muscle fibers bind the last portions of the two seminal vesicles together. The muscle fibers which separate the epithelium of the median walls of the posterior, constricted ends of the seminal vesicles terminate abruptly, and the two tubes unite to become the ejaculatory duct.

Just prior to the beginning of the ejaculatory duct, the epithelium of the constricted, posterior end of each seminal vesicle is elevated into two folds, a mid-dorsal fold and a mid-ventral fold. With the disappearance of the median, separating wall, these folds are continued into the ejaculatory duct as dorsolateral and ventrolateral epithelial folds (fig. 7).

Sections of the seminal vesicles of the males on nuptial flight show these organs packed with the fibrillar and granular secretion; the cellular lining appears converted entirely to the secretion, as in holocrine glands. It is practically impossible to find the nuclei of the epithelial cells except at the anterior and posterior ends of the seminal vesicles. Here, where the nuclei are present, they are small, compact, and flattened against the basement membrane. The outer walls of the end portions of the seminal vesicles, just before the beginning of the ejaculatory duct, have developed a deep fold or invagination which involves both the epithelial and the muscle layers. Here, on the median walls, only the epithelia project into the lumina. These projections practically occlude the lumina (fig. 19).

Ejaculatory duct and wedge (figs. 2, 3, 4, and 18). The ejaculatory duct is lined entirely with simple epithelium, which is built on a distinct basement membrane.

In the anterior portion of the duct, the cells which cover the dorsal and the ventral lateral folds are columnar in shape, the cells at the bases of and between these folds are low cuboidal or squamous in shape, and high cuboidal- or columnar-shaped cells line the lateral walls (fig. 7). The dense cytoplasm of the cells contains occasional, small secretion vacuoles in the supranuclear portions of the cells. In this anterior portion of the duct, the epithelial folds which extend into the lumen give the lumen a very irregular shape. The extent of these folds varies with the individual; in some, the folds practically fill the lumen, and, in others, the epithelial folds are lower and the lumen is more open. Here, the muscle layer is a well-developed band of circularly or obliquely arranged fibers surrounding the epithelium. A few longitudinal fibers, two or three to begin with and more farther on, are found on the dorsal side between the circular muscle and the epithelial layers. These longitudinal muscle fibers are situated approximately at the bases of the dorsolateral folds.

Examination of serial sections of the ejaculatory duct in a posterior direction shows a sudden increase in the height of the ventrolateral folds so that they almost touch the dorsal wall laterad of the dorsolateral folds; this is the first indication of the wedge. A thin, chitinous layer covers the dorsal ridges of these ventrolateral folds. The chitin becomes thicker and extends down over the whole outer walls of the folds (fig. 8). These chitinous sheets form the arms or the wings of the wedge. The outer or lateral and the inner epithelial layers of the ventrolateral folds separate from each other to form a space. This separation starts at the top of the folds and continues ventrally. The epithelium underlying the chitin of the arms becomes lower in height until it is a flat, squamous epithelium, while the epithelium of the inner surfaces of the folds and of the floor between the folds remains unchanged. A little farther back, the ventral part of the chitinous arms extends outward at right angles; in cross section, the left chitinous arm assumes an S-curve and the right one a reversed S-curve. At this level, the epi-

thelium of the inner surfaces of the folds and of the floor of the duct is suspended from the dorsal ridges, and it is composed of cuboidal-shaped cells. This epithelium becomes elevated slightly as the lower portions of the arms curve toward and approach one another (fig. 9). The bottom curve of each arm is, at this level, the only portion firmly attached to the wall of the ejaculatory duct. From the lower curves of the arms, a chitinous projection grows mediad from each side to meet and fuse in the middle. This is the beginning of the junction of the two arms of the wedge. The thin, squamous epithelium of the inner surfaces of the arms covers the upper and lower sides of this median connection (fig. 10). The lower portions of the opposing wedge arms converge, fuse, and then terminate (fig. 11). From this region posteriorly, the upper portions of the arms converge to form the point of the wedge, and this point is not attached to the walls of the ejaculatory duct but lies free in the lumen. In cross section, the chitinous arms assume a wide V-shape. The layer of cuboidal-shaped epithelial cells is still suspended between the dorsal ridges of the arms, and the thin layer of squamous epithelium still adheres to the inner surfaces of the arms. The chitin along the inner margins of the dorsal edges of the arms grows mediad and fuses, and the epithelium underlying this chitin changes from cuboidal- to squamous-shaped cells. In cross section, the wedge becomes roughly triangular in shape with the base of the triangle under the dorsal wall of the duct and the apex pointed ventrally (fig. 12). As the point of the wedge is reached, the cross-sectional shape changes; the sides converge, the height diminishes, and the dorsal surface becomes arched. The outer chitinous surface is longitudinally ridged (figs. 13 and 14).

Changes in the wall of the ejaculatory duct are apparent as the arms of the wedge converge to form the point. The dorsolateral folds reduce in size and then disappear. The cells on the dorsal and ventral walls of the ejaculatory duct become low cuboidal or squamous in shape, while those on the lateral walls remain columnar-shaped. Cross sections of some of

the ejaculatory ducts examined show an indentation of the surface of the epithelium of each lateral wall (fig. 12). This indicates a longitudinal groove extending along each side of the ejaculatory duct. The lumen assumes an oval shape with the long axis in a dorsoventral plane. The longitudinal muscle fibers which were located only on the dorsolateral portions move around the wall and increase in number to form a band of 2 to 4 fibers in thickness on the lateral and ventrolateral walls of the ejaculatory duct. The peripheral, circular fibers reduce to form a covering of about one fiber in thickness dorsally and dorsolaterally. On the ventrolateral and ventral sides of the duct, the outer covering of muscle fibers is not greatly reduced, but it becomes oblique in direction. The ventral wall of the ejaculatory duct opens into the dorsal, posterior end of the aedeagal bladder (figs. 13 and 14). The muscle fibers on the ventrolateral walls change their direction from oblique to longitudinal. They remain longitudinal to the end of the duct. The longitudinal muscle on the dorsolateral walls reduces to a few fibers in thickness toward the end. The ejaculatory duct extends a short distance beyond the end of the wedge. Its posterior end is reduced in height and is incorporated into the dorsal, posterior wall of the aedeagal bladder.

It was noted that, for males on nuptial flight, the epithelial cells at the anterior end of the ejaculatory duct may be more vacuolate.

Aedeagal bladder (figs. 4 and 15). This large, muscular-walled bladder is the only portion of the internal reproductive system with a chitinous intima. The intima is wrinkled, and nuclei of the squamous-shaped, epithelial cells can be seen scattered between its small, irregular folds. The aedeagal bladder opens posteriorly and dorsally into the sperm gutters, and the intima of the bladder is continuous with the chitinous lining of the sperm gutters and the median surfaces of the inner valves. A well-developed muscle layer of large fibers arranged longitudinally and obliquely covers the epithelium and forms the outer coat of the bladder. However, muscle

fibers are absent on the posterior, mid-ventral region of the bladder and also on the posterior, mid-dorsal portion of the bladder, which comes in contact with the ventral surface of that portion of the ejaculatory duct containing the wedge (figs. 9 through 14). These fibers which form the muscle coat of the aedeagal bladder are wider in diameter than the muscle fibers surrounding the other organs of this reproductive system. Histologically, they have more the appearance and texture of the muscles of the body wall segments. The muscles on the dorsal wall of the bladder with which the muscle fibers from the posterior end of the ejaculatory duct mingle are attached to the dorsal side of the sperm gutters (fig. 16). The lateral muscles are attached to the outer walls of the sperm gutters, while the ventral and ventro-lateral muscle fibers on each side are attached to the distal ends of the aedeagal apodemes of the inner pair of genitalic valves (fig. 2). The lumen of the aedeagal bladder contains a large secretion mass, which is a finely granular, basophilic secretion (fig. 4).

No differences have been observed between the aedeagal bladders of the males collected from the nests and those collected on the nuptial flight. The granular secretion mass is still present and in about the same amounts in both groups of males.

Aedeagal gland (fig. 17). On the dorsal and dorsolateral walls of the sperm gutters, just posterior to the termination of the muscle fibers of the aedeagal bladder, there are arranged 18 to 20 large, spherical- or subspherical-shaped cells. These cells constitute the aedeagal gland. Each gland cell has a large, compact, centrally located, spherical nucleus and finely granular, acidophilic cytoplasm. A short, fine duct leads from each cell. These ducts are collected into a common duct for each side or into two or three ducts for each side. The common ducts open dorsolaterally into the sperm gutters.

DISCUSSION

The male reproductive system of *C. pennsylvanicus* agrees in its anatomy with this system in *C. ligniperdus* as reported

by Adlerz (1886), and it is generally similar to this system in *Formica rufa* (Meinert, 1861).

Testes and vasa efferentia. The paired testes in the higher Hymenoptera lie close to the mid-dorsal region of the abdomen above the midgut, and they are usually surrounded by a membranous covering, the testicular capsule.

In the formicine ants, each testis is composed of tubular- or saccular-shaped follicles. *C. pennsylvanicus* has 12–16 saccular-shaped follicles, while *C. ligniperdus* has 17 small tubular-shaped follicles, and *Formica sanguinea* has 21 (Adlerz). Meinert reports 20 follicles in *Formica rufa,* 14 in *F. exsecta,* and 7 in *Lasius niger.* Adlerz states that in the myrmicine ants the testis generally has three follicles, larger and more bulbous-shaped than those in the formicines. He reports three follicles in each testis for *Leptothorax acervorum, Anergates atratulus,* and *Formicoxenus nitidulus,* Meinert reports three in *Myrmica ruginodis,* while Janet ('02) reports 4 in *M. rubra.* Muckerjee ('27) gives no number for *Dorylus labiatus,* but he says there are a fair number of minute, uniform follicles in each testis, which his illustrations show to be tubular in shape. According to Marcus ('53), the testis of *Dorymyrmex emmaericaellus* consists of one compact follicle with a network of canals inside it, while the testis of *Pogonomyrmex marcusi* has 6 follicles. In the vespids and the honeybee, each testis consists of 200–300 follicles, while in other bees and wasps there are usually 1 to 4 follicles in each testis (Bordas, 1895, D'Rosario, '42, and Machida, '34).

Although scattered spermatozoa are present in the lumina of the testes follicles and the vasa efferentia of *C. pennsylvanicus,* most of the sperm is arranged in the vasa deferentia. No meiotic stages were identified in the sections of the testes examined. This agrees with the recent observations of Whelden and Haskins ('53) for *C. pennsylvanicus* and other ants. Janet reports that the follicles of the adult male of *M. rubra* are packed with bundles of sperm. Muckerjee states that in *Dorylus labiatus* the anterior part of the vas deferens is filled with sperm. Marcus reports bundles of sperm in the canals

inside the testis follicle of *Dorymyrmex emmaericaellus.* These observations indicate that the production of sperm is accomplished before the individual reaches the imaginal stage. This pattern of sperm development has been reported in the honeybee (Bishop, '20, and Zander '51) and in the wasp, *Polistes fadowigae,* by Machida ('34). The granular masses which have been observed in the distal ends of some of the follicles and lying over many of the follicles in *C. pennsylvanicus* may be an indication of the loss of activity of the follicles.

The short vasa efferentia, which lead from the testes follicles in *C. pennsylvanicus,* are collected into a common duct. This common duct has been referred to as the reservoir by Janet ('02) in *M. rubra* and by Koschewnikoff (1891), Bordas (1895), Michaëlis ('00), and Bishop ('20) in the male Hymenoptera investigated by them.

Capsule of testes. A single, testicular capsule covers the testes of *C. pennsylvanicus.* Adlerz reports that the testes of *C. ligniperdus* are surrounded by a common peritoneal covering, which has many tracheal branches penetrating it. Meinert observed a testicular covering in *Formica rufa,* which he refers to as the scrotum (ascribed to Léon Dufour, 1841, Mém. pres. à l'Acad. Roy. Sci. Inst. France, vol. 7: 267–647). Adlerz further mentions a peritoneal covering surrounding the testes of *Formicoxenus nitidulus.* On the other hand, Janet does not describe a capsule in *M. rubra,* nor does Marcus mention a capsule in *Pogonomyrmex marcusi* or *Dorymyrmex emmaericaellus.* Muckerjee states that the testes of *Dorylus labiatus* are not enclosed within a membrane.

Bordas (1895) indicates that, in practically all of the higher Hymenoptera, a single testicular capsule covers both testes but that in a few genera each testis has its own covering. There is considerable variation in the thickness of the capsule for the different families and subfamilies. In all cases, however, the capsule is richly supplied with tracheal branches, and the larger of these branches apparently aid in holding the capsule and the testes in position. This latter condition is reported for *C. pennsylvanicus.*

The histological study of the testicular capsule in the honeybee by Koschewnikoff (1891) appears to be the most comprehensive for the higher Hymenoptera. Koschewnikoff states that the capsule of the honeybee is composed of two envelopes; the outer one is formed by the fat body and the inner one is more connective-tissue in nature. He further divides the inner envelope into two layers; the outer layer has large cells with oval nuclei, and the inner layer is composed of fine fibers with spindle-shaped nuclei. Tracheae penetrate all the coverings and ramify between the testes follicles. Severin and Severin ('08) describe the capsule in the sawfly, *Cimbex americana,* as follows: ". . . the club-shaped testicular follicles are surrounded by a thin membrane which contains small ovoid nuclei. Numerous tracheae penetrate this membrane and branch and rebranch in the space between the testicular follicles. A delicate network of loose fibrous connective tissue is present in the space between the testicular follicles." In *C. pennsylvanicus,* the capsule is not divided into coats or layers. Some scattered fat cells are found on the periphery, but these do not form a distinct layer. The whole capsule resembles more the inner layer of the inner envelope of the honeybee and the capsule of the sawfly. However, the "fine fibers" of the honeybee are, in *C. pennsylvanicus,* bundles of branching tracheoles, and the spindle-shaped nuclei are the nuclei of their epithelial covering (fig. 5). The stellate-shaped cells seen between the bundles of tracheae and tracheoles are connective in nature and are probably the tracheal end cells or transition cells, which have been observed to form membranes around the internal organs of insects (Wigglesworth, '50, p. 225).

The importance or meaning of the basophilic, multinucleate cells found in the capsule is not known. They might have some endocrinal function, or they might be haemocytes enmeshed in the branching tracheoles.

Vas deferens. The arrangement of the vasa deferentia in *C. pennsylvanicus* appears to be the same as that of *C. ligniperdus* reported by Adlerz. In both, the anterior ends are

twisted and convoluted and are covered by the testicular capsule; the posterior portions are rather straight. Adlerz states that the lumina of the vasa deferentia have a cuticular covering; there is no covering of the epithelium in the lumina of these vessels in *pennsylvanicus*. Meinert indicates that in *F. rufa* the first part of each vas deferens is bent laterally and that the posterior ends are straight. He refers to these posterior ends as the stalked or stem portions of the vasa deferentia although there is no apparent difference in the diameter of any portion of these tubes. It appears from the reports of Meinert, Adlerz, and Janet that the course of the vasa deferentia in the myrmicines is more direct than in the formicines. Muckerjee found that in *Dorylus labiatus* the first portion of each vas deferens is straight and has a spherical dilation which is packed with mature spermatozoa; these tubes then make a U-turn and dilate to form the seminal vesicles. In *Dorymyrmex emmaericaellus* the thin walls of the vasa deferentia enlarge and become more muscular as they approach the seminal vesicles (Marcus, '53).

This present study reveals that in *pennsylvanicus* the mature sperm are stored in the vasa deferentia and are prevented from moving along the system by a granular plug in the lumina of the constricted posterior ends of the vessels (fig. 6). Even the males which were collected on the nuptial flight show this same condition of the system. This might indicate that copulation is the stimulus which moves the sperm.

Seminal vesicles. The shape, size, and arrangement of the seminal vesicles of *C. pennsylvanicus* agree with those of *C. ligniperdus* as reported by Adlerz. He states that the epithelium of the seminal vesicles consists of circular cells, that there is no distinct lumen, and that these organs are covered by a layer of fine, circular muscle fibers. The seminal vesicles of the *pennsylvanicus* males collected in the spring have a distinct lumen, which is being filled with the basophilic, fibrillar and granular secretion of the high columnar-shaped epithelial cells. In the males collected on the nuptial flight, most of the epithelium of the seminal vesicles has been converted

to the secretion which packs the lumina of these organs. The fibers of the muscle layer are fine and are arranged obliquely and circularly.

These organs show variations in size, shape, and arrangement within the system in the ants investigated. In *F. rufa* (Meinert) they are similar in shape to those of *C. ligniperdus* and *pennsylvanicus,* but apparently they are smaller. In *Leptothorax acervorum, Anergates atratulus,* and *Formicoxenus nitidulus,* the seminal vesicles, although generally similar to those in *pennsylvanicus,* are somewhat more globose in shape and may be more widely separated from each other (Adlerz). In *Myrmica ruginodis,* they have the same shape as in *Leptothorax acervorum,* but they are not as large and are more widely separated (Meinert). *M. rubra* and *Dorymyrmex emmaericaellus* have spherically-shaped seminal vesicles (Janet, '02 and Marcus, '53). The vasa deferentia usually open into the posterior, ventral, mediad surfaces of the seminal vesicles. However, in *M. rubra* and *Dorylus labiatus* they open into the anterior ends of the seminal vesicles, and this seems to be the arrangement in *Dorymyrmex emmaericaellus.*

The males of *pennsylvanicus* collected on the nuptial flight have the lumina of the end portions constricted by deep folds of the walls (fig. 19). Whether these folds serve as a device to hold the secretion within the seminal vesicles or whether they have a further purpose in the functioning of the system is not clear at this time.

Ejaculatory duct and wedge. In most of the ants so far studied, the common duct formed by the union of the posterior ends of the seminal vesicles is the ejaculatory duct. However, in *Dorylus labiatus* the seminal vesicles join with the bases of the corresponding accessory glands, whose posterior ends unite to form the ejaculatory duct (Muckerjee). Accessory glands are prominent organs of the male reproductive system of most of the higher Hymenoptera (Bordas, 1895) and are also found in the honeybee (Bishop, '20).

The opening of the ejaculatory duct into the dorsal, posterior end of the aedeagal bladder, as observed in *C. pennsylvanicus,* is similar to the arrangement described by Clausen ('38) for *Formica rufa.* A chitinous wedge in the ejaculatory duct was noticed by Clausen while he was examining the ejaculatory duct and genitalia of *F. rufa.* In this ant, it is about 360 μ in length by 310 μ in width with the posterior point unattached in the lumen of the last part of the ejaculatory duct; the arms of the wedge are attached to the ventral wall and extend into the lateral walls. Clausen refers to this structure as a constricting wedge or sperrkeil. A wedge was observed in *C. pennsylvanicus* with the same shape and general arrangement as in *F. rufa*; measurements indicate that it is smaller, about 300 μ in length by 180 μ in width. Marcus reports a chitinous angle in the posterior end of the ejaculatory duct of *Acromyrmex sylvestrii* arranged with its apex pointed posteriorly, but he gives no further information about it. He also states that in this ant the median wall at the junction of the seminal vesicles is extended into the lumen of the ejaculatory duct. His accompanying illustration shows this as a small spear-shaped extension, which he considers directs the spermatic fluid. He mentions that a circular muscle coat surrounds the ejaculatory duct. In *C. pennsylvanicus* the outer muscle coat is circular in the anterior and middle portions but changes to oblique and longitudinal in the posterior portion.

Marcus observed a thin, chitinous sac protruding from the ends of the inner genitalic valves of the males of *Dorymyrmex emmaericaellus,* which he claims is a modification of the ejaculatory duct. He believes that the gray, granular secretion in this sac probably serves as the fluid to move the sperm in the female tract. He found this structure in two other dolichoderines, *Conomyrma brunnei* and *Forelius* sp. Clausen ('38) mentions that when he fixed some *Bothromyrmex* males in alcohol, they ejected a rather large plug of material from the end of the genitalia as they were dying. This material was chiefly an amorphous mass containing spermatozoa and some muscle fibers; these latter were probably torn from the

walls of the last part of the tract. Clausen says this plug is covered, dorsally, by the thin, chitinous membrane which unites the inner valves.

Aedeagal bladder. Meinert makes no mention of an aedeagal bladder in his description of the male system in *F. rufa,* but Clausen, in his study of the same species, reports a penis bladder. Adlerz found this structure in *C. ligniperdus,* and he refers to it as the penis. The description which Clausen gives of the position of this organ in *F. rufa,* the relation of the ejaculatory duct to it, and its relation to the inner valves of the genitalia agree with the description for *C. pennsylvanicus* in this paper. Clausen also states, but with no explanation, that the penis bladder and its continuation between the inner valves constitutes the penis. An amorphous secretion mass is found in this bladder in *F. rufa,* while in *C. pennsylvanicus* the secretion is finely granular and basophilic.

No comparable organ has been reported in any of the myrmicines or other ants investigated. Marcus reports a small, saccular accessory gland which lies dorsal to the ejaculatory duct in *Acromyrmex sylvestrii.*

Aedeagal gland. In his study of *M. rubra,* Janet described unicellular, integumentary glands located in the inner genitalic valves just below their dorsal covering; these he called the penial gland. He did not report the number of cells which compose the gland. However, his figure A, Plate 15, which is a sagittal section through the inner valves and which might therefore represent only half the gland, illustrates 15 cells in the group. He states that the ducts of the cells have not been followed with certainty but that they appear to open separately into the space between the inner valves. Clausen describes and figures penis glands in *F. rufa* in the same position as Janet reports them in *M. rubra.* He, too, gives no indication of the number of cells of the gland, and he has no description of the ducts. In *C. pennsylvanicus* there are 18 to 20 fairly large cells in the gland, and the ducts open on the dorsolateral margins of the inner valves into the sperm gut-

ters. Marcus reports prominent aedeagal glands in *Conomyrma brunnei* and *Forelius* sp.

Function of the wedge. Clausen considers that the purpose of the wedge is to constrict the lumen of the ejaculatory duct. He assumes that the sperm moves down the system and is collected in the aedeagal bladder prior to mating and that, as the muscles of the aedeagal bladder contract to force the sperm outward, the wall of the ejaculatory duct becomes pressed against the wedge. Thus, the duct is closed so that the sperm and fluids in the bladder have only one exit, which is between the inner surfaces of the laminae aedeagales and the thin uniting dorsal wall. The observations for *C. pennsylvanicus* show that even on the nuptial flight the sperm is still in the vasa deferentia. It seems highly probable that the sperm remains here until mating occurs since the posterior ends of the vasa deferentia are plugged and the lumina of the posterior portions of the seminal vesicles are constricted. Bishop ('20) observed in the honeybee that the lumina of all parts of the male reproductive system are not entirely open or continuous prior to copulation and that the spermatozoa, the seminal fluid, and the mucous of the accessory gland are not mixed before then.

The purpose of the wedge might be to separate the secretion of the seminal vesicles and the spermatozoa into two lateral streams or masses and to divert this material into the sperm gutters; the arrangement of the wedge in the lumen of the duct and its posterior position in the ejaculatory duct seem to indicate this (figs. 4 and 18). Material moving along the lumen would be separated as it moves over the point of the wedge and would be guided by the epithelial grooves on the lateral walls of the posterior part of the duct; the unattached posterior point of the wedge is also longitudinally ridged (figs. 10 through 14). The opening of the ejaculatory duct on the dorsal, posterior wall of the aedeagal bladder and the disposition and the insertion of the muscles of this posterior end of the reproductive tract on the median walls of the inner valves suggest that the contraction of these muscles would

pull the end of the ejaculatory duct close to the beginning of the sperm gutters. Further, there are no muscle fibers on the mid-dorsal side of the aedeagal bladder which comes in contact with the ventral surface of that portion of the ejaculatory duct containing the wedge. Thus, there is no interference with the activities of the ejaculatory duct in the region of the wedge as the seminal fluids are moving along. The secretion of the aedeagal bladder is probably the first material to leave the male reproductive system and to enter the female system.

SUMMARY

1. The anatomy and the histology of the male reproductive system of the carpenter ant, *Camponotus pennsylvanicus* DeGeer, is described from specimens collected from nests during the spring and from specimens taken on a nuptial flight.

2. The system in *C. pennsylvanicus* agrees in its anatomy with this system in *C. ligniperdus* as reported by Adlerz, and it is generally similar to this system in *Formica rufa* as reported by Meinert.

3. The testes lie in the mid-dorsal region of the gaster above the ventriculus of the digestive system. The 12–16 small, spherical, saccular follicles of each testis open by means of short vasa efferentia into a common duct, which is reflected to form the much wider vas deferens.

4. A granular mass is situated over the free end of almost every testis follicle. This mass is attached by granular strands to the basement membrane of the follicle, or it is joined with similar granules which may take the place of the cells at the blind end of the follicles.

5. The common capsule which surrounds the testes is composed of a network of branching tracheae and anastomosing bundles of tracheoles. Stellate-shaped cells with long processes located between the tracheae and the bundles of tracheoles appear to constitute the connective tissue. Occasionally, fairly large, multinucleate cells can be seen embedded in the capsule.

6. The vasa deferentia are filled with spermatozoa, which are arranged spirally around the lumina. The posterior ends of these tubes are constricted slightly just before they enter the ventral, mediad surfaces of the seminal vesicles. The lumen of this constricted region is plugged with an acidophilic, non-cellular secretion of the epithelium.

7. The columnar-shaped epithelial cells of the prominent seminal vesicles give rise to the basophilic, fibrillar and granular secretion which fills these organs. The tapering, posterior ends of the seminal vesicles unite to form the ejaculatory duct. The males taken on nuptial flight show the outer walls of these end portions with deep folds, which practically close the lumina.

8. In the lumen of the latter portion of the ejaculatory duct, there is a chitinous, Y-shaped wedge. The arms of the wedge arises from the outer walls of the ventrolateral epithelial folds of the duct, and the point of the wedge lies free in the lumen of the posterior end of the duct. The muscle coat of the duct consists chiefly of circularly or obliquely arranged fibers at the anterior end and of longitudinally arranged fibers toward the posterior end. The posterior end of the ejaculatory duct becomes incorporated into the dorsal, posterior wall of the aedeagal bladder.

9. The aedeagal bladder is a muscular sac situated beneath the ejaculatory duct. It is the only organ of the male system which has a chitinous intima. The fibers of its muscular coat are wider in diameter than the muscle fibers of the other organs of the male system, and they have more the appearance and texture of the body wall muscles. This bladder opens posteriorly and dorsally between the median walls and into the sperm gutters of the inner genitalic valves. It contains a finely granular, basophilic secretion.

10. The aedeagal gland, present on the dorsal and dorsolateral walls of the sperm gutters, consists of 18 to 20 cells. The ducts from these cells open dorsolaterally into the sperm gutters.

11. Anatomical and histological comparisons are made with the reproductive organs of ants and other higher Hymenoptera previously reported.

12. It is suggested that the purpose of the granular plug in the constricted ends of the vasa deferentia and the folds of the outer walls of the posterior ends of the seminal vesicles is to hold the spermatozoa and the secretions of the organs in their proper positions until mating occurs.

13. It is suggested that the function of the wedge in the ejaculatory duct is to divide the seminal fluid and the spermatozoa into two lateral masses and to direct this material into the sperm gutters of the inner genitalic valves.

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PLATES

ABBREVIATIONS

A, anus
Aa, aedeagal apodeme
Ab, aedeagal bladder
Ad, aedeagus
B, basement membrane
C, cuspis volsellaris
Ca, capsule of testis
Cr, crop
D, digitus volsellaris
Da, dorsal surface of aedeagus
E, epithelium
EA, epithelium of aedeagal bladder
Ed, ejaculatory duct
EF, dorsolateral epithelium folds
F, follicle of testis
Fe, follicular cell
G, granular mass
Ge, aedeagal gland cells
H, heart
I, intestine
In, intima of aedeagal bladder
L, lamina aedeagalis
La, lamina annularis
Lp, lamina parameralis
M, muscle
Ma, Malpighian tubule
Mc, circular muscle
Ml, longitudinal muscle
Mo, oblique muscle
Mn, multinucleate cells
N, nerve cord
P, pygostyle
Pm, paramere
Pv, proventriculus or gizzard
R, rectum
S, sperm gutter
Sc, stellate cells
Se, secretion of seminal vesicles
Sm, secretion mass
Sp, sperm head and spermatozoa
Sv, seminal vesicle
T, testis
To, tracheoles
Tr, trachea
Vd, vas deferens
Ve, vas efferens
Vn, ventriculus
W, wedge
II-X, Roman numerals indicate abdominal segments

PLATE 1

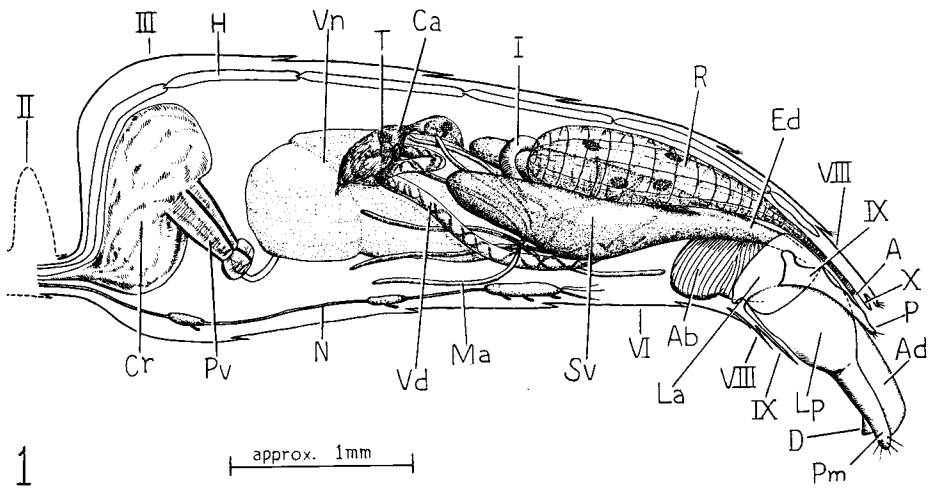
EXPLANATION OF FIGURES

1 Diagram of a lateral dissection of the gaster of the male of *Camponotus pennsylvanicus* DeGeer showing the internal organs in position. The left side of the IXth and Xth terga and the left lateral genitalic valves are still in position. Roman numerals on the dorsal side indicate the terga, and those on the ventral side indicate the sterna.

2 Dorsal view of the male reproductive system and genitalia. The right testicular capsule has been removed.

3 A reconstruction of the wedge removed from the ejaculatory duct and viewed dorsolaterally.

4 Lateral dissection of the posterior end of the reproductive system. The right inner genitalic valve, the lamina aedeagalis, has been removed. The position of the wedge in the ejaculatory duct is indicated.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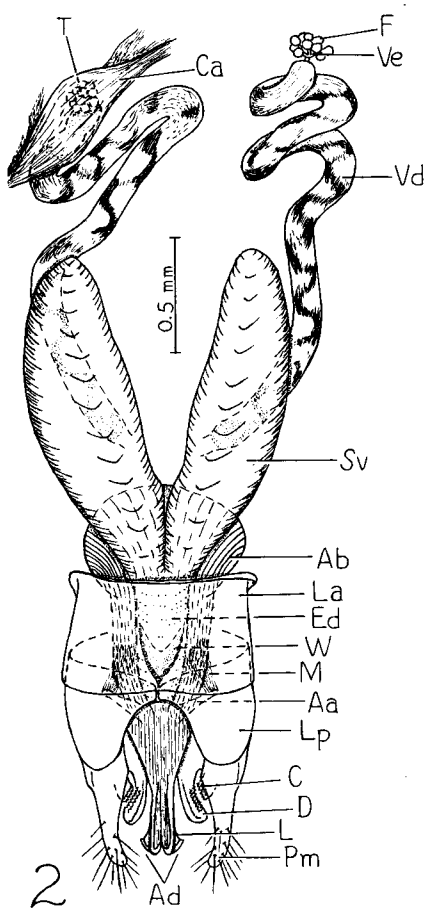
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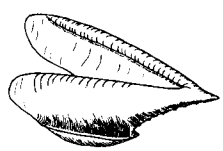

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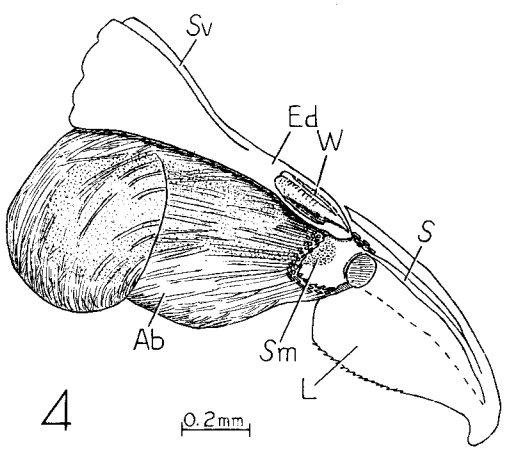
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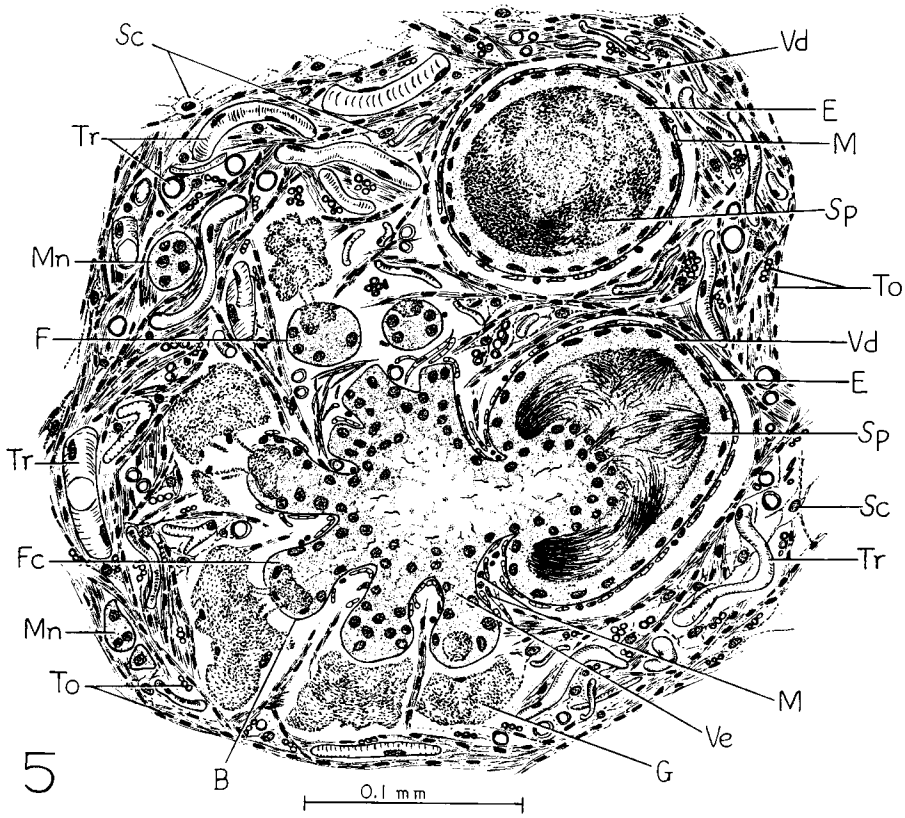
PLATE 2

EXPLANATION OF FIGURES

5 Section of the testis and the testicular capsule at the junction of the vasa efferentia and the vas deferens.

6 Longitudinal section of the posterior constricted portion of the vas deferens and its entrance into the seminal vesicle. The lumen of this posterior end of the vas deferens is plugged with an acidophilic, non-cellular secretion. The break in the section indicates a small portion has been omitted.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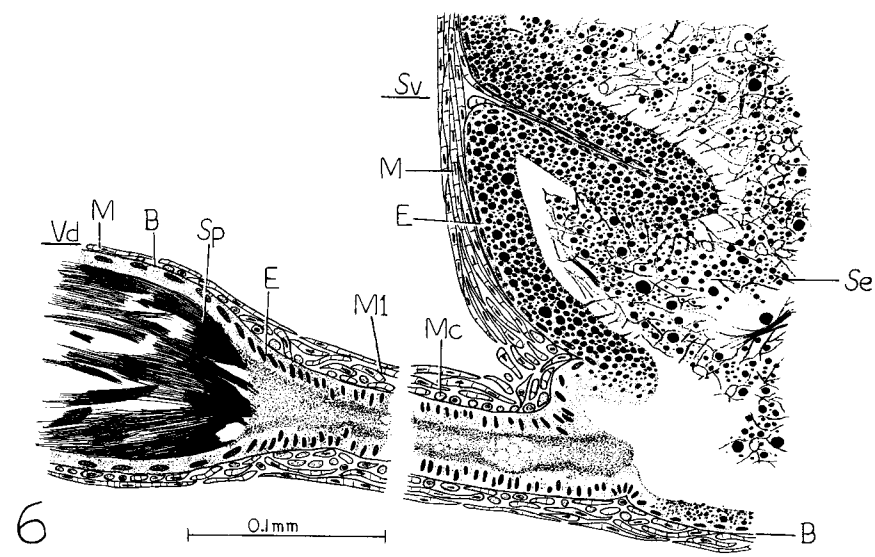
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PLATE 3

EXPLANATION OF FIGURES

Figs. 7–14. A series of sections through various levels of the ejaculatory duct, which shows the arrangement of the wedge in the duct. The bottom layer of each section is the dorsal wall of the aedeagal bladder.

7 A section of the duct anterior to the wedge. 8. A section through the anterior part of the arms of the wedge. 9 and 10. Sections through the region of the wedge where the arms are converging. 11. A section through the wedge just posterior to the convergence of the arms. 12, 13, and 14. Sections through the point of the wedge. The last two sections show the entrance of the ejaculatory duct into the aedeagal bladder.

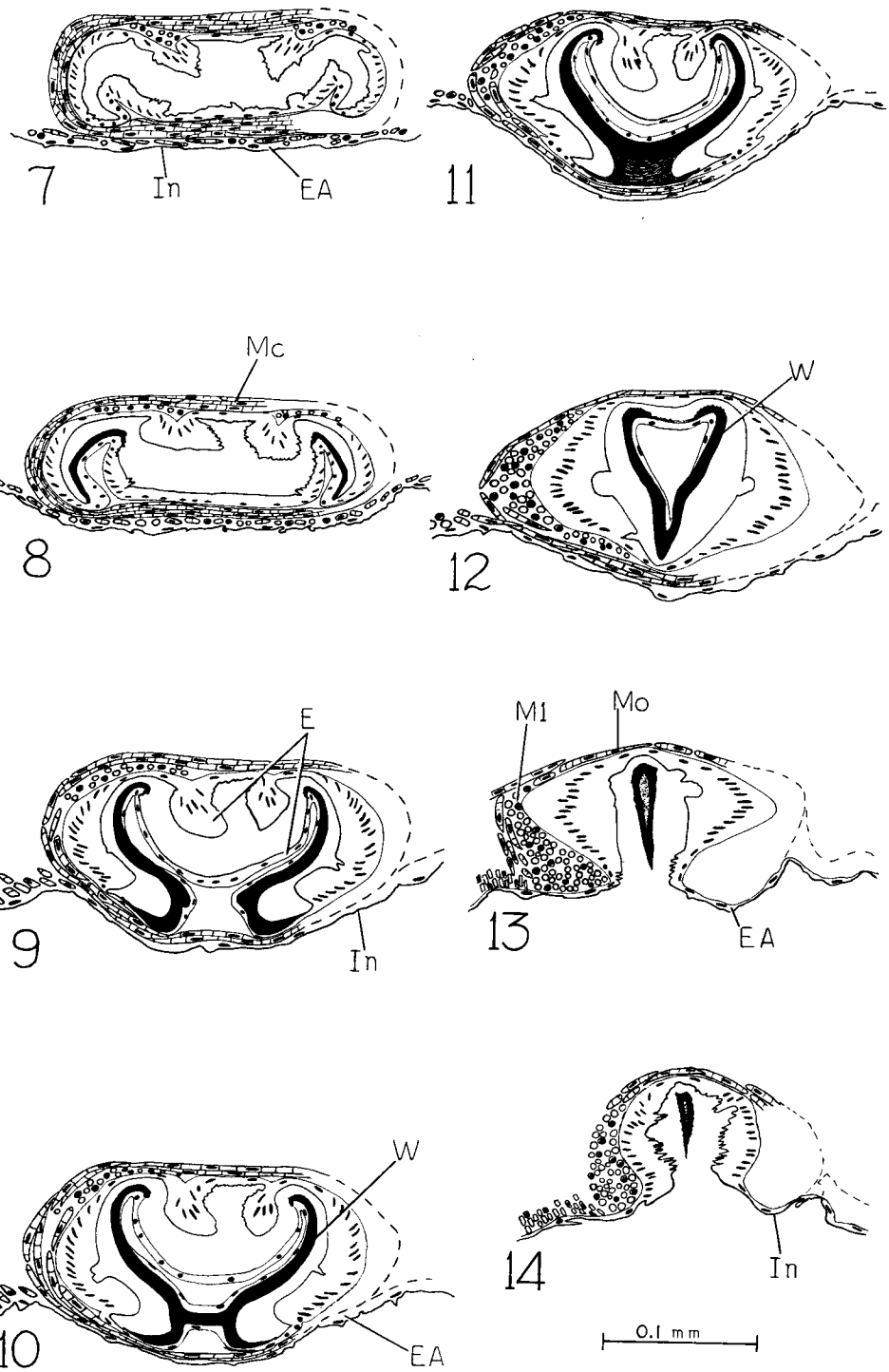
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PLATE 4

EXPLANATION OF FIGURES

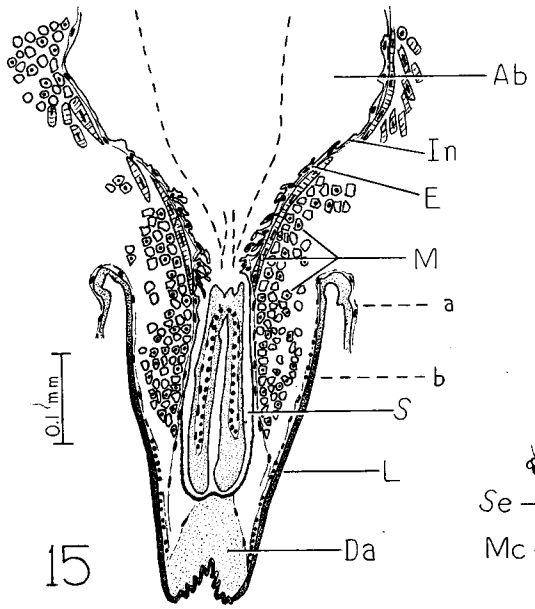
15 A frontal view of the junction of the aedeagal bladder and the inner genitalic valves, the laminae aedeagales. The broken outline in the aedeagal bladder indicates the position of the ejaculatory duct, which lies dorsal to this level.

16 A cross section of the inner genitalic valves taken at about level *a* of figure 15. This shows how the aedeagal bladder opens into the sperm gutters of the inner valves.

17 A cross section of the inner genitalic valves taken at about level *b* of figure 15. This section shows the position of the aedeagal gland.

18 A dorsal view of the posterior ends of the seminal vesicles joining and forming the ejaculatory duct. The wedge is placed in the duct, and the broken lines indicate the lumina of the tubes.

19 A frontal section through the end portions of the seminal vesicles of a male on nuptial flight, which shows the deep folds of the outer walls and the epithelial ridges on the inner walls.



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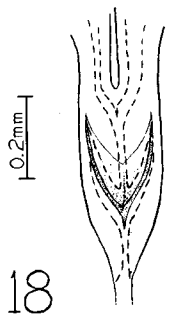

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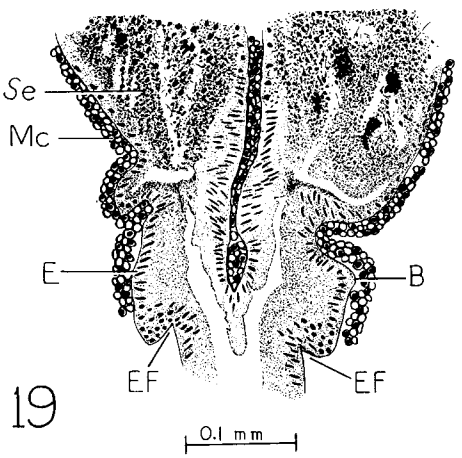

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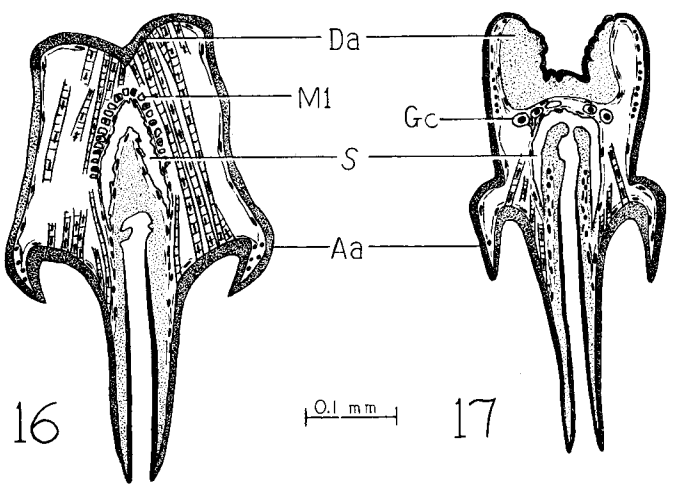

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